

***Colophospermum* reduced to *Hardwickia* (Leguminosae-Caesalpinioideae)**

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ABSTRACT

The genus *Colophospermum*, described in 1949, known from its only species *C. mopane* from southern Africa, is congeneric with the monotypic *Hardwickia* described from India in 1811. The new combination *H. mopane* is made. The taxonomic study is accompanied by a palynological as well as a wood anatomical study.

MOTS CLÉS
Colophospermum,
Hardwickia,
Inde,
Afrique méridionale,
Mopane.

RÉSUMÉ

Le genre *Colophospermum*, décrit en 1949, connu par son unique espèce *C. mopane* d'Afrique tropicale méridionale, paraît congénérique de *Hardwickia*, genre monotypique décrit de l'Inde en 1811. La nouvelle combinaison *H. mopane* est proposée. L'étude taxonomique est accompagnée des résultats de recherches palynologiques et anatomiques du bois.

Hardwickia was described by ROXBURGH and illustrated in his *Plants of the Coast of Coromandel* in 1811, based on *H. binata* (Fig. 1). Two more species *H. pinnata* Roxb. ex DC. (1825) and *H. alternifolia* (Elm.) Elm. (ELMER 1907, 1908) were described later, but afterwards both proved to belong in the genus *Kingiodendron* Harms (KNAAP-VAN MEEUWEN 1970) ren-

dering the genus monotypic again. *Hardwickia* differs from *Kingiodendron* notably in having only two leaflets with flabellately arranged nerves and in lacking bracteoles on the flower stipe. Also, the wood of *Hardwickia* differs significantly from that of *Kingiodendron* in lacking axial gum ducts (KNAAP-VAN MEEUWEN 1970).

LÉONARD (1949) described *Colophospermum* to



Hardwickia binata

Fig. 1.—*Hardwickia binata*: plate 209, reproduced from ROXBURGH (1811).

accommodate the aberrant *Copaifera*? (*Colophospermum*) *mopane* Kirk ex Benth. BENTHAM (1865a), on account of having fruiting material only, did not want to describe it as a genus distinct from *Copaifera*, although KIRK, the collector of the type, suggested this, and proposed *Colophospermum* as its name. LÉONARD's original publication of *Colophospermum* does not show

that any comparison was made with extra African genera, although *Copaifera* as well as *Hardwickia* were currently classified (BENTHAM 1865b; TAUBERT 1894) in the same tribe namely Cynometreae, which are now named Detarieae. Most characters which are mentioned by LÉONARD to distinguish *Colophospermum* from *Copaifera* are in fact characters that characterize

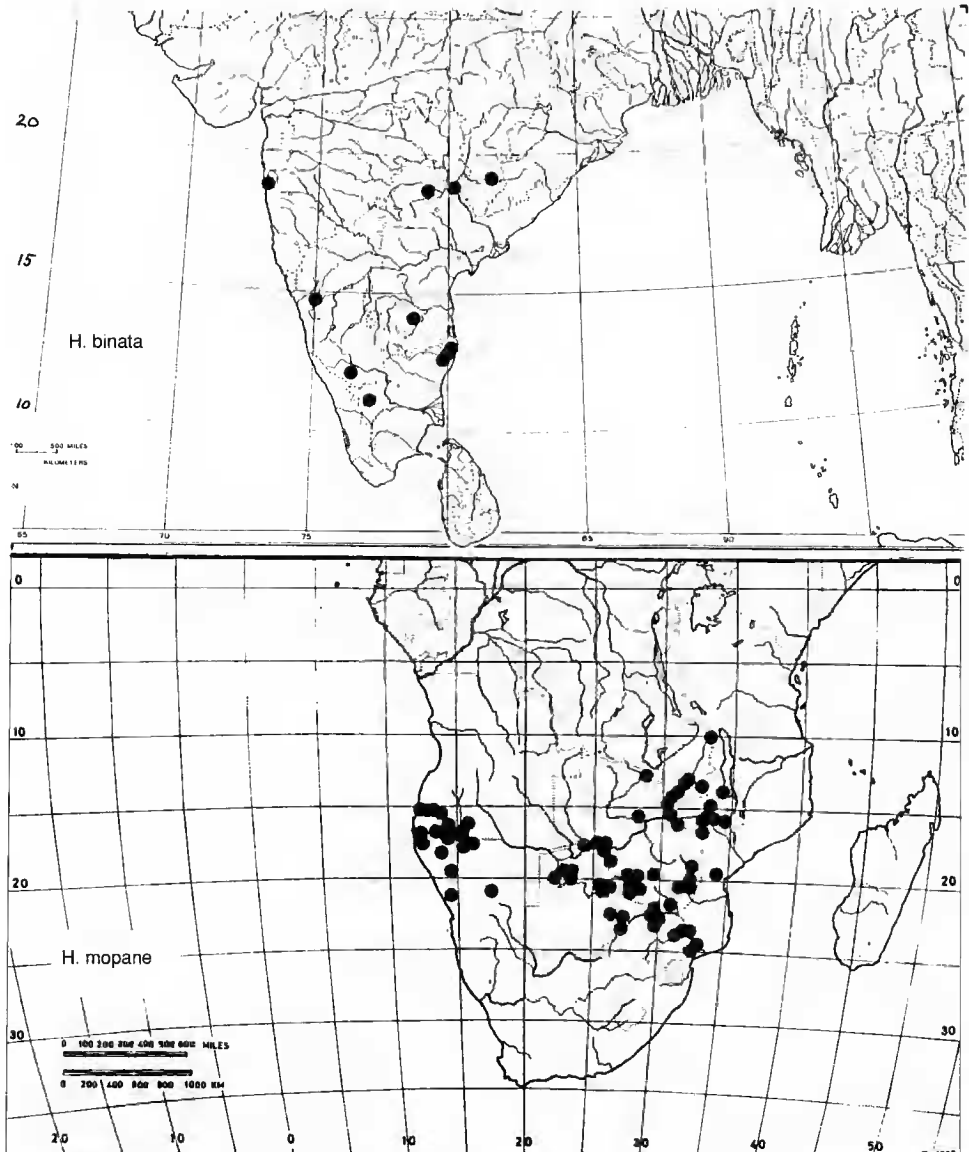


Fig. 2.—Distribution of *Hardwickia binata* (above) and of *H. mopane* (below).

Hardwickia, such as the foliaceous "prolongation" of the leaf rachis, the absence of bracteoles, the single ovule, and the corrugated cotyledons. More characters that are common to both genera can be added, such as those found in the pollen structure (GRAHAM & BARKER 1981; this paper) and in the basic chromosome number (GOLDBLATT 1981). The characters shared by *Colophospermum* and *Hardwickia* are listed below. Added, are the characters in which both taxa differ.

Characters common to *Colophospermum* and *Hardwickia*

Leaves 2-foliolate with a much reduced, deciduous, united, secondary pair of leaflets in between.

Leaflets with translucent dots.

Flowers without bracteoles.

Flowers actinomorphic, apetalous.

Filaments long, thread-like, anthers large, versatile.

Stigma large, \pm peltate.

Ovary with 1 ovule only.

Seeds narrowly winged, furrowed.

Cotyledons corrugated.

Cotyledons epigeous.

Wind pollinated.

Chromosome number $n = 17$.

Differences between *Colophospermum* and *Hardwickia*

Colophospermum: 4 sepals; 20-25 stamens; seed \pm reniform, with resin vesicles.

Hardwickia: (4-)5 sepals; 10(-11) stamens; seed straight, without resin vesicles.

A number of the characters shared by the two monotypic genera are quite unique in the Detarieae or even in the Caesalpinioideae. As such may be mentioned the lack of bracteoles on the flower stipe, the flower and pollen structure that indicates wind pollination, and the chromosome number. The foliaceous appendage on the leaf may be added. This "prolongation" of the leaf beyond the pair of fully developed leaflets is foliaceous, conduplicate and mostly soon deciduous. The morphology is the same in both genera. In the original publication of *Colopho-*

spermum, LÉONARD (1949) did not express his opinion about the morphological nature of this element, but later he named it a terminal foliole (LÉONARD 1957). CUSSET (1970) was certain that it represents a foliole. In this paper the foliar element is indicated as a much reduced, secondary pair of united leaflets, not a single terminal leaflet. This is more in accordance with the paripinnate nature of the leaves. Moreover, the cotyledons in *Colophospermum*, whether they are true cotyledons or paracotyledons (DE VOGEL 1979), look like a pair of united leaflets, when theervation pattern is considered. As such they appear the same as the reduced pair of leaflets.

Two characters, viz the uniovulate ovary and the corrugated cotyledons, are also found in the following genera: *Gossweilerodendron*, *Kingiodendron*, *Oxystigma* and *Prinria*, in which the latter has more or less flat cotyledons.

KNAAP-VAN MEEUWEN (1970) described the *Hardwickia* leaflets as without pellucid dots. However, *Hardwickia* also has pellucid dots, although they are much less numerous and less distinctive.

The ecology of *Hardwickia binata* (ROY 1996) is rather similar to that of *Colophospermum mopane* (ROSS 1977; MAPAURE 1994) as both taxa are encountered in rather dry savannas, the first in India north of the equator, the second south of the equator in southern Africa (Fig. 2).

POLLEN MORPHOLOGY

(by I.K. FERGUSON).

The pollen morphology of the two monotypic genera *Hardwickia* (*H. binata*) and *Colophospermum* (*C. mopane*) has only been described comparatively recently. FASBENDER (1959) described the pollen of *Hardwickia* as tricolporate. This would appear to be based on an incorrectly identified specimen. VAN ZINDEREN BAKKER & COETZEE (1959) described *Colophospermum* as pantoporate. It was not appreciated that these two taxa had similar pantoporate pollen until GRAHAM et al. (1980) drew attention to the unusual pollen and further described the pollen of the two taxa (GRAHAM & BARKER 1981) but without drawing taxonomic conclusions.

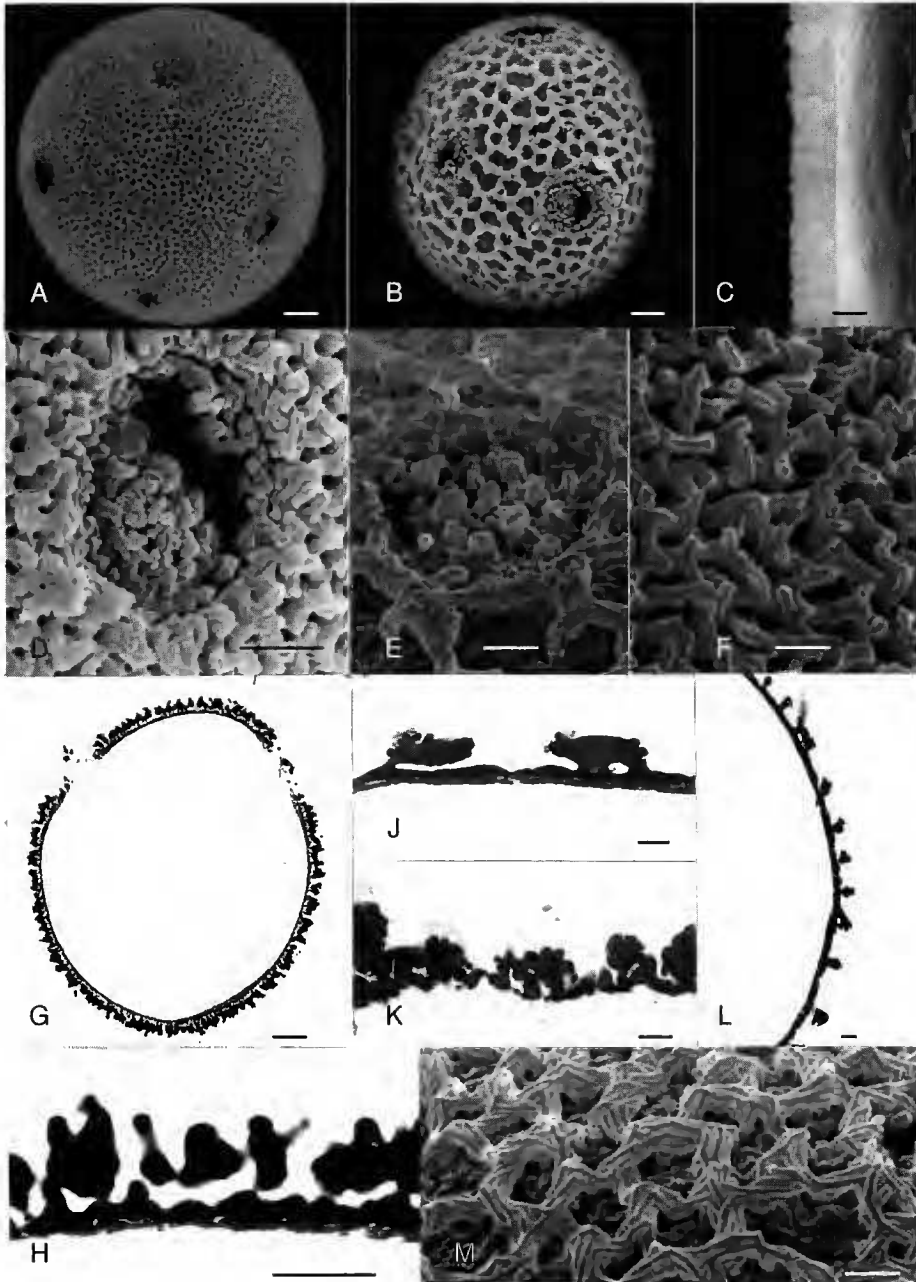


Fig. 3.—A, C, D, F, G, H, *Hardwickia binata*; B, E, J-M, *H. mopane*: A, pantoporate pollen with microreticulate exine; B, pantoporate pollen with reticulate exine; C, detail of exine stratification showing thick sexine and thin nexine; D, detail of pore with aperture membrane; E, detail of pore with aperture membrane; F, exine ornamentation showing scabrate muri; G, thin section of whole pollen grain showing 2 apertures and thin nexine; H, thin section detail of exine stratification with thin endexine, clear foot layer, columellae layer, thick tectum with scabrate surface; J, thin section detail of exine stratification with thick columellae; K, thin section detail of aperture membrane; L, thin section of part of pollen showing thin nexine and widely spaced sexine elements; M, exine ornamentation showing striate muri. (A, C, D, G, *Khan 2319*; B, J-L, *Lugard 243*; E, M, *Torre 7326*; F, *Gamble 874*. A-F, L, SEM micrographs; G-K, TEM micrographs. Scale A, B, G = 10 μ m; C-F, H-M = 1 μ m).

FERGUSON (1987) in a study of the exine stratification emphasized that similarity in the details of the pantoporate apertures and the very thin exine. He suggested, and it was supported further by GUINET & FERGUSON (1989), that the thin walled pantoporate pollen might be associated with wind pollination, citing the suggestion of ROSS (1977) that *Colophospermum* is wind pollinated.

Hitherto no taxonomic evaluation of the two taxa incorporating pollen morphological data has been made.

Materials and methods

Material was obtained from the Herbarium, The Royal Botanic Gardens, Kew (K). The pollen samples were prepared by the methods described by FERGUSON et al. (1994). SEM = Scanning electron microscope, TEM = Transmission electron microscopy.

General pollen description.—Fig. 3.

Pollen spheroidal, 36–50 µm in diameter, pantoporate with 8–12 pores 5–7 µm in diameter, pores with a granular or rugulate membrane. Ornamentation reticulate or microreticulate/rugulate. Exine 1–1.5 µm thick, nexine thin, sexine well developed 1 µm or greater thick. In TEM endexine thin, foot layer distinct, columellae short and tectum well developed ca. 1 µm thick.

Colophospermum (Fig. 3B, E, J–M).

Pores 6–7 µm in diameter with a granular membrane. Ornamentation reticulate, lumina (1.5)2–4(–5) µm on the longest axis, muri distinctly striate. Columellae comparatively sparse and thick.

SPECIMENS EXAMINED.—Botswana: *Lugard* 243; Mozambique: *Torre* 7326.

Hardwickia (Fig. 3A, C–D, F–H).

Pores ca. 5 µm in diameter with a comparatively finer scabrate membrane than *Colophospermum*. Ornamentation microreticulate/rugulate, lumina about or less than 0.5 µm on the longest axis, muri scabrate giving a somewhat overall rugulate appearance to the surface of the exine.

Columellae comparatively denser and thinner.

SPECIMENS EXAMINED.—India: *Gamble* 874, *Gamble* 15258, *Khan* 2319.

Discussion

The pantoporate pollen is remarkable, occurring very rarely not only in the Caesalpinoideae where it occurs in the two species under investigation and in one or two species of *Bauhinia*, but also occurring only in 2 genera of Papilionoideae (GUINET & FERGUSON 1989).

The similarity in the structure of the apertures, the aperture membrane, pollen size, shape and thin exine are especially noteworthy. The exine ornamentation and stratification differs sufficiently to allow the pollen of the two species to be easily distinguished. Nonetheless the reticulate pattern, thin exine and its stratification are basically very similar.

Previous workers have noted the similarities in pollen morphology (GRAHAM et al. 1980; GRAHAM & BARKER 1981; FERGUSON 1987) but drew no taxonomic conclusions. GUINET & FERGUSON (1989) emphasized the unique pantoporate pollen type in the Caesalpinoideae and suggested that the pollen might be a secondary adaptation to wind pollination.

Modification of exine ornamentation as a development of pollination strategy has been suggested by a number of authors as a widespread syndrome in both Papilionoideae and Caesalpinoideae (FERGUSON & SKVARLA 1982; FERGUSON & PEARCE 1986; GUINET & FERGUSON 1989; KLITGAARD & FERGUSON 1992). The occurrence of this unique pantoporate pollen type in two geographically isolated species could be interpreted as a convergent modification to wind pollination. However, it is significant that the occurrence of this unique pantoporate pollen in the two geographically isolated species agrees well with several macromorphological features, some quite unique as well. Therefore these common morphological features could support the view that the similar pollen type found in *Hardwickia* and *Colophospermum* may indeed be indicative of relationship. This relationship may in turn underlie the expression of a secondary modification to wind pollination.

WOOD ANATOMY (by P.E. GASSON & B.J.H. ter WELLE).

Colophospermum mopane is a medium-sized to large tree, usually ca. 10 m tall, but ranging from 4-18 m. It is dominant in large areas of hot, low-lying, mainly alluvial, but also alkaline and poorly-drained soils, and often forms pure stands. The heartwood is dark reddish-brown to almost black, very durable, hard and heavy and difficult to work, but subject to termite attack (CUTLER, pers. comm.). It is commonly used for mine props and railway sleepers, and makes very good firewood (COATES PALGRAVE 1988; PRIOR & CUTLER 1996). There is much literature on the species, including several papers with information on wood properties, summarised by TIMBERLAKE (1995).

Hardwickia binata is a moderate-sized to large tree from drier areas. The heartwood is dark red to dark brown, with darker streaks and often with a purplish cast, and is probably the hardest and heaviest Indian wood, which is difficult to work when seasoned (RAMESH RAO & PURKAYASTHA 1972; PEARSON & BROWN 1932). It is used for mine props, posts and beams, cartwheel naves and spokes, ploughs, railway sleepers, and is a moderately good fuelwood. In 1897 *H. pinnata* was transferred by HARMS to *Kingiodendron* (as *K. pinnatum*), although PEARSON & BROWN (1932) still described the two species under *Hardwickia*, viz. *H. binata* and *H. pinnata*. *Kingiodendron pinnatum* is characterized by the presence of axial gum canals and non-crystalliferous axial parenchyma and GAMBLE (1902) states that the tree (which he calls *H. pinnata*) also yields a valuable balsam like copaiba. These characters are all indications validating the transfer by HARMS (1897) of *H. pinnata* to another genus. A wood anatomical description of *Hardwickia* is provided by JUTTE (1965) who studied some genera of the Cynometreae.

Colophospermum mopane (Fig. 4).

Growth rings distinct, marked by tangential lines of axial parenchyma one to two cells wide.

Vessels diffuse, solitary (8-38%), usually in radial multiples of 2-4, occasionally to at least 12, sometimes in 2 immediately adjacent rows,

or in irregular clusters of 2-6, round to oval, 19-47(15-67) per sq. mm, diameter 52-80(12-108) µm. Vessel element length: 161(45-271) µm. Perforations simple. Intervascular pits alternate, vested, round or oval to polygonal, sometimes elongated, often with coalescent apertures, 2-5 µm. Vessel-ray and vessel-parenchyma pits similar, but half-bordered. Yellow to dark-brown organic deposits common to abundant.

Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls, lumen up to 5 µm in diameter, walls up to 2-4 µm thick. Very few fibres gelatinous. Length: 600(465-725) µm in Kw7103.

Axial parenchyma scanty paratracheal, incompletely vasicentric, vasicentric-aliform (lozenge-type), some diffuse, and terminal tangential bands one to two cells wide. Crystalliferous chambered parenchyma strands with prismatic crystals abundant, up to 19-24 crystals per strand. These strands very often in contact with the rays. Strands 2-4 cells long.

Rays 7-8(5-10) per mm, 2(-3)-seriate, few uniseriate, the uniseriate rays up to 7-8 cells (= 140-150 µm) high, the multiseriate rays up to 16-27 cells (= 310-440 µm) high, homocellular, composed of procumbent cells. Yellow to brown organic deposits common to abundant.

SPECIMENS EXAMINED.—Zimbabwe: *J. Prior s.n.*; *Rhodesia 12.1954* (Kw 7103); Botswana: *Terry et al. 185* (Kw 72242); Angola: *Dechamps et al. 1194* (Uw 23528); Namibia: *Pettinen s.n.* (ex RHBw 14016); South Africa: *CSIR IND. 78* (ex RHBw 15178).

Hardwickia binata (Fig. 5).

Growth rings distinct, marked by tangential lines of axial parenchyma one to several cells wide.

Vessels diffuse, solitary (22-100%), and in radial multiples of 2-3, occasionally up to 6, round to oval, 6-9(3-13) per sq. mm, diameter 77-108(12-173) µm. Vessel element length: 137(60-217) µm. Perforations simple. Intervascular pits alternate, vested, round to oval, occasionally with coalescent apertures, 2-5 µm. Reddish-brown deposits common.

Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls,

lumen up to 7.5 μm in diameter, walls 2.5-7.5 μm thick. Fibres often gelatinous, but not found in Kw7306. Length: 875-994(390-1469) μm (280-1700 μm in PEARSON & BROWN 1932). Axial parenchyma scanty paratracheal and

incompletely vasicentric, occasionally forming lateral wings (i.e. winged aliform), also diffuse and in terminal tangential lines, in Kw21524 many tangential bands up to 10 cells wide. Crystalliferous chambered parenchyma strands

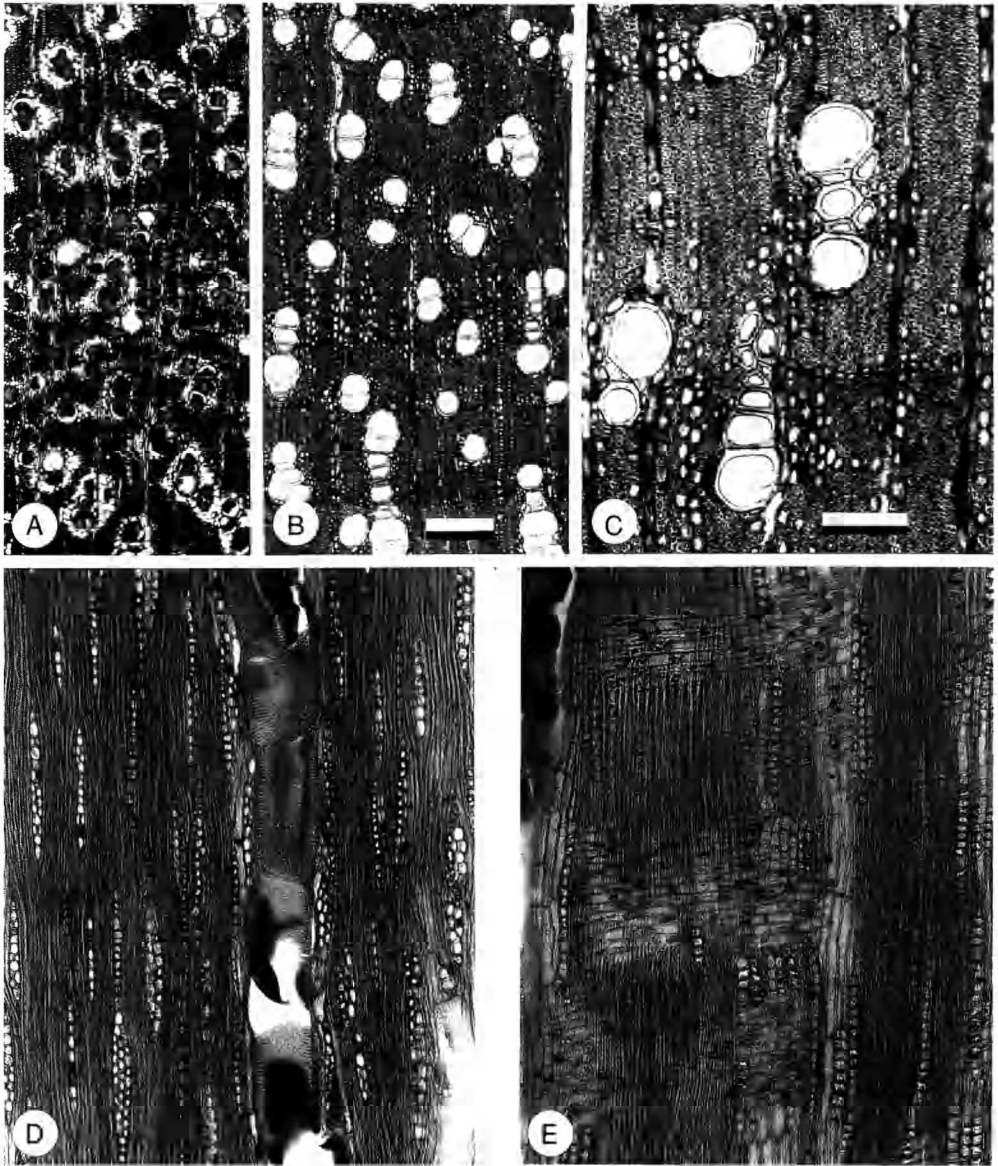


Fig. 4.—*Hardwickia mopane*: (A, D, E, Uw23528; B, C, Kw7103). A-C, transverse sections showing vessel distribution and axial parenchyma patterns; D, tangential longitudinal section showing ray width and height, chains of prismatic crystals, many immediately adjacent to rays, and vessels with pitting and dark contents; E, radial longitudinal section showing procumbent ray cells and chains of prismatic crystals. Scale lines: For A-B (on B) is 200 μm ; for Figs C-E (on C) is 100 μm .

with prismatic crystals abundant, up to 15 crystals per strand. These strands usually bordering the rays. Strands 2-4 cells long.

Rays 4-9 per mm, 3-4-seriate, up to 22 cells high (= 420-540 μm), homocellular, composed

of procumbent cells. Brown organic deposits common.

NOTE.—Kw7303 has abundant traumatic canals in wide axial parenchyma bands, finer

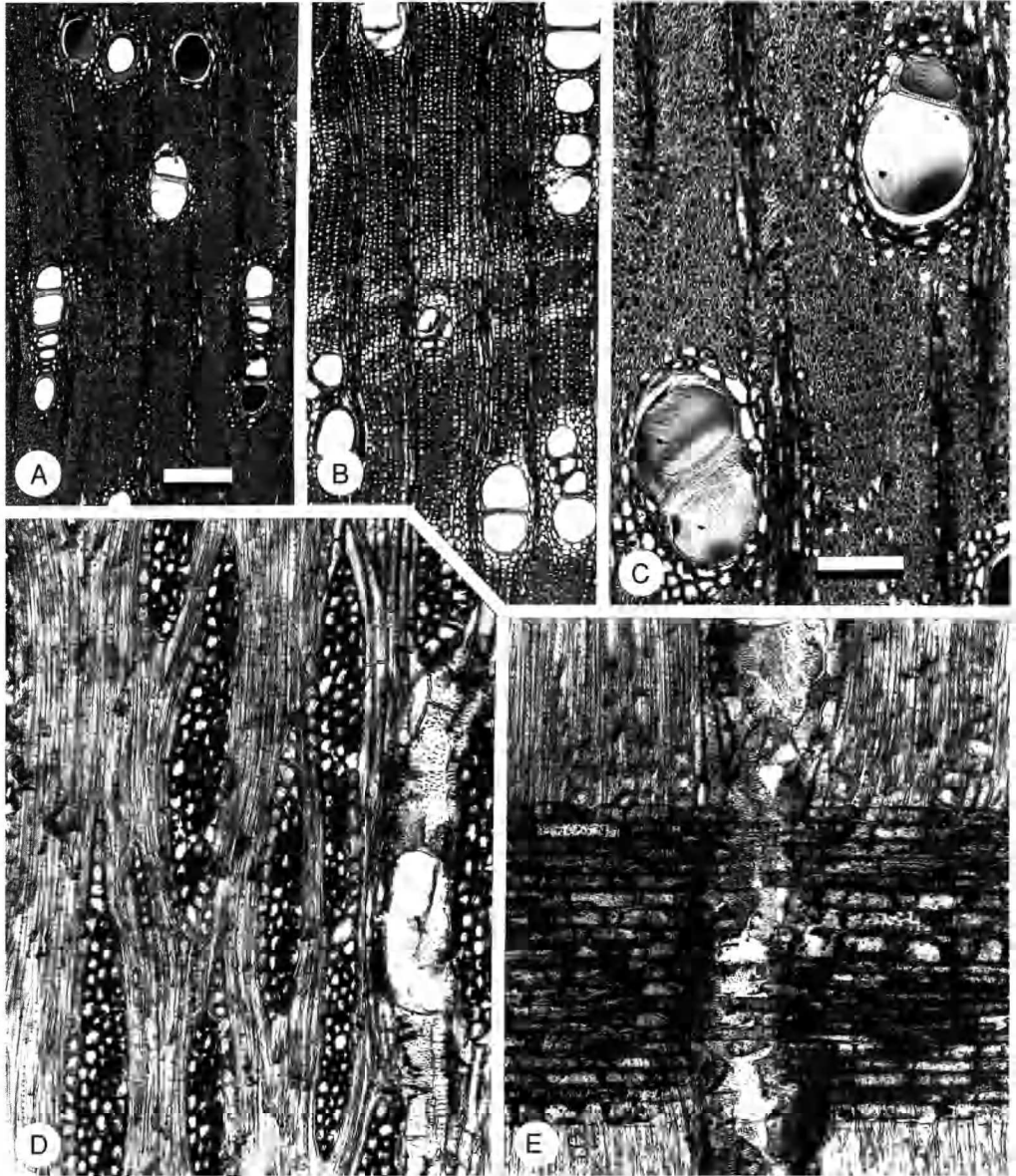


Fig. 5.—*Hardwickia binata*: A-C, transverse sections showing vessel distribution and axial parenchyma patterns; D, tangential longitudinal section showing ray width and height and chains of prismatic crystals mainly adjacent to rays; E, radial longitudinal section showing procumbent ray cells, intervessel and vessel-ray pitting, and chains of prismatic crystals. Scale lines: For Figs A, B (on A) is 200 μm , for Figs C-E (on C) is 100 μm . All Royal Botanic Gardens, Calcutta, 1868.

intervessel pitting, axial parenchyma strands of considerably more than 4 cells, and prismatic crystals in ray cells. This combination of characters strongly indicates that this sample is incorrectly named. PEARSON & BROWN (1932) refer to KANEHIRA (1924) reporting horizontal (i.e. radial) gum canals in the wood.

SPECIMENS EXAMINED.—Calcutta: *Anderson 1868*, cultivated in Royal Botanic Gardens (Kw7306); *Gamble 143*, Madhya Pradesh (Kw 21523); *Gamble 4020* (see *Gamble 1902*), Coimbatore (Kw 21524); *East India Museum* (Kw 7303), this sample is misidentified (see note above).

The wood anatomy of the two genera is very similar in most respects. Vessels are diffusely arranged, and there tend to be more radial multiples in *Colophospermum*. However, the greater proportion of solitary vessels in *Hardwickia* is partly explained by their larger size, with fewer vessels per mm². The intervessel pitting is very similar in both genera. The fibres are thick-walled, with virtually no lumina in both, and gelatinous fibres are variably present. Axial parenchyma patterns are variable within each species, but the overall range from scanty paratracheal to more abundant paratracheal, and diffuse parenchyma are present in both genera. This range of parenchyma distribution is found in many legume genera. Prismatic crystals are abundant in both, and are often found in chambered parenchyma cells directly adjacent to the rays. The rays are slightly wider in *Hardwickia*, but in many taxa, variation in ray width is not unusual. Both have homocellular rays composed of procumbent cells. Organic deposits are common in both, although they are of different colours (yellow-brown in *Colophospermum*, brown to reddish-brown in *Hardwickia*). In the absence of chemical tests, the significance of these differences is not known. The differences in quantitative characters (i.e. vessel diameter and element length, vessel density and fibre length) may all be attributable to differences in cambial age of the samples, since the *Hardwickia* samples were all

from mature trunk wood, whereas the *Colophospermum* samples were from narrower stems. This could also explain the more frequent vessel groupings in *Colophospermum*, since such groupings tend to be more frequent in narrower stems and branches.

The wood of the two taxa is very similar anatomically, but there are many examples in the legumes of taxa that look similar but are not particularly closely related. In this case, the lack of a feature (axial canals) is probably very important. In the legumes these are found only in Detarieae and Amherstieae, including, in COWAN & POLHILL's (1981) *Crudia* group of the Detarieae, *Kingiodendron pinnatum* (once included in *Hardwickia*), *Prioria*, *Oxystigma* and *Gossweilerodendron* (see table in GASSON 1994; BARETTA-KUIPERS 1981; ILIC 1991; WHEELER et al. 1986). These genera are all grouped by BRETELER (1996) in the apetaliferous *Hymenaea* complex of the Detarieae. If *Colophospermum* and *Hardwickia* truly belong in this group, then it is likely that they are more closely related to each other than to the genera with axial canals. Although *Colophospermum* lacks canals, the wood is reported by SMITH & SHAH-SMITH (in press) to be resinous, presumably as a result of contents in the lumina of the vessels and parenchyma cells.

After these studies, it is concluded that the two genera have to be united under the name *Hardwickia*.

TAXONOMY (by F.J. BRETELER).

HARDWICKIA Roxb.

Pl. Coromandel 3: 6, t. 209 (1811).—Type: *H. binata* Roxb.

Colophospermum Kirk ex J. Léonard, Bull. Jard. Bot. Brux. 19: 390 (1949).—Type: *C. mopane* (Kirk ex Benth.) Kirk ex J. Léonard.

This genus contains two species which may be distinguished as follows:

Leaflets obscurely pellucid-dotted, with 4-6 palmately arranged nerves; flowers with (4-)5 sepals and with 10 (-11) stamens; fruit straight, strap-shaped, with a proximal wing. India *H. binata*
 Leaflets very distinctly pellucid-dotted, with 8-11 palmately arranged nerves; flowers with 4 sepals and with 20-25 stamens; fruit curved, reniform, with a very narrow wing at one side. Southern tropical Africa .. *H. mopane*

Hardwickia binata Roxb.

Pl. Coromandel 3: 6, t. 209 (1811).—Type: *t.* 209 (ROXBURG 1811). For additional references see KNAAP-VAN MEEUWIEN (1970).

SPECIMENS EXAMINED.—INDIA: *Beddome* 2550, Cuddapah Hills (BM); *Herb. Benthamianum s.n.*, N.W. Bengal, ? Tilorhue (K); *Bourne* 2154, Clingleput distr., Kambakan (K); *Bourne s.n.*, Mysore, near Hangal (K); *Buchanan s.n.*, Mysore (BM); *Forest Service s.n.*, Coimbatore (L, WAG); *Gamble* 11086, Madras, Auaukapur, Muchakola (K); *Gamble* 15258, Madras, Kotealeota (K); *Haines* 5615, Bihar, near Daltongang (K); *Herb. Madras* 9963, Mamandur (K); *Hooker & Thomson* 299, Bihar, upper part of Soane (K); *Jacquemont* 237 (P); *Lusington (Herb. Gamble) s.n.*, Madras, Somanaparam (K); *Mauheue & Paramasivam RHT* 24304, Dharmapuri, Kambalai (K); *Matthew & Paramasivam RHT* 24305 (L); *Mooney* 239, Narepa, Telagu (K); *Mooney* 2143, Bastar State, Pilur (K); *Khan in Herb. Mooney* 2319, Bastar State, Bhopalpatnam (K); *Pierre* 122, Coromandel (P); *Roxburgh s.n.* (BM); *Fischer in herb. Sedgwick & Bell* 5957, N. Bombay (K); *Wight* 874, Madras (K, P, WAG).—Cultivate: *Andersen* 28, Botanical Garden Calcutta (P); *Japin* 2780, Hyderabad, Miami forest (K); *Pierre s.n.*, Botanical Garden Calcutta (P); *Wood s.n.* (K).

Hardwickia mopane (Kirk ex Benth.) Breteler, **comb. nov.**

Copaifera? (*Colophospermum*) *mopane* Kirk ex Benth., Trans. Linn. Soc. London 25: 317, t. 43A (1865).—*Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard, Bull. Jard. Bot. Brux. 19: 390 (1949).—Type: *Kirk s.n.*, Mozambique, Lupata (holo-, K!). For additional references see LÉONARD (1949).

SPECIMENS EXAMINED.—ANGOLA: *Bamps et al.* 4086, Km 54 Roçadas-Pereira d'Eca (WAG); *Barbosa* 9778, Moçamedes, Caraculo (K); *Brito et al.* 7843 A, Huila, Roçadas, Cumato (WAG); *Couto* 191, Cunene, Roçadas, Chicusse Chama (K); *Couto* 370, Km 92 Sa da Bandeira-Moçamedes (K); *Dechamps et al.* 1193, 1194, Moçamedes, near Capangombe (K, WAG); *Exell & Mendonça* 2339, Moçamedes, Birei (BM); *Exell & Mendonça* 2880, Huila, between Donguna and Ruacana (BM); *Gossweiler* 11.000, Moçamedes, Mubi-Bero (K); *Grandvaux Barbosa & Correia* 9111, Moçamedes, Caraculo (BM); *Humbert* 16492, between Moçamedes and Villa Arriaga (BM, P); *Mendes* 1133, Huila, Quihita (BM); *Mendes* 1722, Huila, Cahama (BM); *Menezes & Henriques* 4, Huila, Cureca (K); *de Menezes* 1036, Huila, Gambos (BM, K, P); *de Menezes* 1403, Huila, Mupa (BM, K, P); *de Menezes*

3661, Huila, Gambos (BM, K, P); *Pearson* 2562, between Gambos and Cahama (K); *Powell-Cotton* 1529, Huila, Cuamaro (BM); *Santos* 153, Moçamedes Dois Irmãos (BM); *C.F. & J.D. Ward* 45, Moçamedes, Tona Nat. Park (K); *Welwitsch* 605, near Bumbo (BM, K, P).—BOTSWANA: *Allen* 249, 255, Orapa (K); *de Beer* 85, Scrowe (K); *Drummond* 5272, Madisara (K); *Erens* 200, Martins Drift Trading Station (K); *Erens* 308, Maun Camp, Thamalakane R. (K); *Iwley* 1081, Moremi (K); *Leach & Noel* 257, Radisele (K); *Lugard* 243, Ngamiland (K); *Lugard* 296, near Tklakane Pits (K); *Miller B* 113, Kazangulu (BM); *Paterson* 30, Makarikari-pan (K); *Pule Evans* 3219, Seruli (BM, K); *Smith* 1226, Thamalakane R. (K); *Yalala* 145, Palapye (K).—MALAWI: *Rurt* 5999, Shire Valley (BM, P).—MOZAMBIQUE: *Correia & Marques* 915, Gaza, Canicado (WAG); *Gomes e Sousa* 4771, Chioca (K); *Grandvaux Barbosa & Carvalho* 3161, 3166, Salima (K); *Grandvaux Barbosa & Carvalho* 3263, 40.5 km Tete-Chioca Rd. (K); *Grandvaux Barbosa & Carvalho* 3279, 76 km Tete-Chioca Rd. (K); *Grandvaux Barbosa & Carvalho* 3408, 38 km Chioca-Chetima Rd. (K); *Grandvaux Barbosa & Carvalho* 3448, Massamba (K); *Grandvaux Barbosa & Carvalho* 3595, 59 km Furancungo-Regulo Bene Rd. (K); *Grandvaux Barbosa & Lemos* 8191, Massingir (K); *Grandvaux Barbosa & Lemos* 8625, 14 km Mabalane-Mapai (K); *Kirk s.n.*, Lupata (K, type); *Livingstone s.n.* (K); *Mendonça* 4038, Vila Machado (BM, K); *Pedroão* 227, 239, Mucatine (K); *Pedroão* 287, Chicholo (K); *Torre* 7326, Magude (BM).—NAMIBIA: *Baum* 978, Nakapi (BM, K); *Coppejans* 6534, Outjo (WAG); *de Winter* 3066 (K); *de Winter* 5293, near Ohopaho (K); *de Winter* 9198, Katima (K); *Germishuizen* 2569, 80 km Outjo-Khorixas (WAG); *Gies* 7766, Farm Grootberg (K, WAG); *Immelman* 490, Farm Mosella, Ugab R. (WAG); *Lubenberg* 4905, Okijwarango (K); *Mercmuller* 1422, Outjo (K); *Moss et al.* 2126, Marienfluss (WAG); *Pegel* 90, Brandberg (K); *Rautanen* 432, Hereroland, Okaukuejo (BM, K); *Rautanen* 524, Ondonga (K); *Radin* 2623, 8963, Oshikango (K); *Radin* 9041, NW of Engela (K); *Schinz s.n.*, Ovamboland (K); *Walter* 1033, Outjo (BM).—SOUTH AFRICA: *Andrew* 1275, Venda, Nwandedi Park (K); *Breyer* 18391, Mokutsi (K); *Cocks* 4827, Zoutpansberg (K); *Codd* 4827, (K); *Codd & de Winter* 5570, Letaba (K); *de Winter* 8673, S of Messina (K); *Eicker et al.* 193, Greefswald (K); *Hutchinson* 2303, Dongolo (K); *I.B.P.E.* 1464, Sandy Spruit (K); *I.B.P.E.* 1918, 1960, Messina (K); *Lambinon & Reekmans* 821104, Kruger Park (WAG); *Rogers* 22549, Messina (K); *Schlieben* 9256, Zoutpansberg (K); *Schlieben & Hartmann* 12307, between Mopane and Vivo (K, WAG); *Small* 467, 60 km N of Louis Trichardt (K); *van der Schijff* 3546, Kruger Park, Letaba (K); *van Vuuren* 1625, 37 km N of Louis Trichardt (WAG); *Verdoorn* 2082, Limpopo R. (K).—ZAMBIA: *Angus* 2237, S of Kafue, Kafue R. (K); *Bingham* 7687, Nyamaluma (WAG); *Bush* 60, W

Lupande R. (K); *Fanshawe 735*, Ndola (K); *Gardner 557*, Kazungula (K); *Grant 4509*, near Livingstone (WAG); *Greenway & Trapnell 5604*, Hupane (Chinsenga) (K); *Robson 956*, Changwe (BM); *Rodin 4501*, Victoria Falls (K); *Shantz 412*, (K); *Shantz 439*, Kafue (K); *Swynnerton 1250*, Muchukwana (BM, K); *Symoens 11451*, 10 km S of Livingstone (K); *Trapnell 1823*, Luangwa (K); *van Rensburg KBS 1798*, Kafue R. (K); *van Rensburg KBS 2134*, Fort Jameson (K); *Yilger 603*, Kalambola (K).—ZIMBABWE: *Biegel 791*, Gwelo (K); *Burt-Dury 18121*, Bosoli Siding (BM); *Chase 1482*, Hot Springs (BM); *Chase 2507*, Ndanga (BM, K); *Cosby 1071*, Chipinga (K); *Drummond 6020*, Beitbridge (K); *Exell et al. 444* (BM); *Gibbs 204*, S of Matopo Hills (BM); *Malaisse 12177*, Beitbridge-Victoria Rd. (WAG); *Mason s.n.*, Victoria Falls (K); *Myres 853*, Odzi R. (K); *Norrgrann s.n.*, Dombodema (WAG); *Obermeyer 2371*, Birchenough Bridge (K); *Phipps 2414*, Mkumburu R. (K); *Plowers 1536*, Nyamandhlovu (K); *Rushworth 1459*, Wankie (K); *Shantz 414*, Tjolojjo (K); *Soane 232*, Sabi Valley (K); *Stace 1482* (K); *Wild 2372* (K).—Cultivate: *Fanshawe 9070 & 9389*, from forest nursery (K).

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REFERENCES

BARETTA-KUIPERS T. 1981.—Wood anatomy of Leguminosae: its relevance to taxonomy: 677-705, in POLHILL R.M. & RAVEN P.H. (eds.), *Advances in Legume Systematics 2*. Royal Botanic Gardens, Kew.
 BENTHAM G. 1865a.—Description of some New Genera and Species of Tropical Leguminosae. *Trans. Linn. Soc. London* 25: 316-317.
 BENTHAM G. 1865b.—Cynometreae (Leguminosae): 584-587, in BENTH. & HOOK, *Gen. Plant.* 1.2.
 BRETELER F.J. 1996 (ined.).—Preliminary classification of the genera of the Detarieae (60 genera).
 COATES PALGRAVE K. 1988.—*Trees of Southern Africa*. Struik Publishers, Cape Town.
 COWAN R.S. & POLHILL R.M. 1981.—Tribe 4, Detarieae DC.: 117-134, in POLHILL R.M. &

RAVEN P.H. (eds.), *Advances in Legume Systematics 1*. Royal Botanic Gardens, Kew.
 CUSSET G. 1970.—Remarques sur des feuilles de dicotylédones. *Boissiera* 16, Genève.
 DE VOGEL E.F. 1979.—*Seedlings of Dicotyledons*. Pudoc, Wageningen.
 ELMER A.D.E. 1907.—Some new Leguminosae. *Leaflets Philipp. Bot.* 1: 223.
 ELMER A.D.E. 1908.—Errata. *Leaflets Philipp. Bot.* 1: 362.
 FASBLINDER M.V. 1959.—Pollen grain morphology and its taxonomic significance in the Amherstieae, Cynometreae and Sclerolobieae (Caesalpinioideae) with special reference to American genera. *Lloydia* 22: 107-162.
 FERGUSON I.K. 1987.—A preliminary survey of the pollen exine stratification in the Caesalpinioideae: 355-385, in C.H. STIRTON, *Advances in Legume Systematics*, 3. Royal Botanic Gardens, Kew.
 FERGUSON I.K. & PEARCE K.J. 1986.—Observations on the pollen morphology of the genus *Bauhinia* (Leguminosae: Caesalpinioideae) in the Neotropics: 283-296, in BLACKMORE S. & FERGUSON I.K. (eds.), *Pollen and Spores: Form and Function*. Academic Press, London.
 FERGUSON I.K., SCHRIRE B.D. & SHEPPERSON R. 1994.—Pollen morphology of the tribe Sophoreae and relationships between subfamilies Caesalpinioideae and Papilionoideae: 53-96, in FERGUSON I.K. & TUCKER S.C. (eds.), *Advances in Legume Systematics 6, Structural Botany*. Royal Botanic Gardens, Kew.
 FERGUSON I.K. & SKVARLA J.J. 1982.—Pollen morphology in relation to pollinators in Papilionoideae (Leguminosae). *Bot. J. Linn. Soc.* 84: 182-193.
 GAMBLE J.S. 1902 (Reprinted 1972).—*A manual of Indian Timbers*. Bishen Singh Mahendra Pal Singh, Dehra Dun.
 GASSON P. 1994.—Wood anatomy of the tribe Sophoreae and related Caesalpinioideae and Papilionoideae: 165-203, in FERGUSON I.K. & TUCKER S. (eds.), *Advances in Legume Systematics 6, Structural Botany*. Royal Botanic Gardens, Kew.
 GOLDBLATT P. 1981.—Cytology and the Phylogeny of Leguminosae: 427-463, in POLHILL R.M. & RAVEN P.H. (eds.), *Advances in Legume Systematics 2*. Royal Botanic Gardens, Kew.
 GRAHAM A., BARKER G. & FREITAS DA SILVA M. 1980.—Unique pollen types in the Caesalpinioideae (Leguminosae). *Grana* 19: 79-84.
 GRAHAM A. & BARKER G. 1981.—Palynology and tribal classification in the Caesalpinioideae: 801-834, in POLHILL R.M. & RAVEN P.H. (eds.), *Advances in Legume Systematics*, 2. Royal Botanic Gardens, Kew.
 GUINET Ph. & FERGUSON I.K. 1989.—Structure, evolution and biology of pollen in Leguminosae: 77-103, in STIRTON C.H. & ZARUCCHI J.L. (eds.), *Advances in Legume Biology Monogr. Syst. Bot.*

- Missouri Bot. Garden* 29. St. Louis, Missouri.
- HARMS H. 1897.—Leguminosae: 190-204, in ENGLER & PRANTL, *Die natürlichen Pflanzenfamilien*, Nachtr. 1, Leipzig.
- ILIC J. 1991.—*CSIRO atlas of hardwoods*. Springer-Verlag, Berlin, etc.
- JUTTE S.M. 1965.—*Cynometreae van de Oude Wereld met uitzondering van Afrika—de houtstructuur*. Internal Report of the Hout Instituut TNO Delft No. H-65-XXI; Optracht 3211/004.
- KANEHIRA R. 1924.—Anat. Notes. Ind. Woods. Govern. Res. Inst. Taihoku, Formosa. *Dept. For. Bull.* 4.
- KLITGAARD B.B. & FERGUSON I.K. 1992.—Pollen morphology of *Brownecopsis* (Leguminosae: Caesalpinioideae), and its evolutionary significance. *Grana* 31: 285-290.
- KNAAP-VAN MEEUWEN M.S. 1970.—A revision of four genera of the tribe Leguminosae-Caesalpinioideae-Cynometreae in Indomalesia and the Pacific. *Blumea* 18: 1-52.
- LÉONARD J. 1949.—Notulae Systematicae. *Bull. Jard. Bot. Brux.* 19: 388-391.
- LÉONARD J. 1957.—Genera des Cynometreae et des Amherstieae africaines (Leguminosae-Caesalpinioideae). *Mem. Acad. Roy. Belg. Sciences* 30: 159-162.
- MAPAURE J. 1994.—The distribution of *Colophospermum mopane* (Leguminosae-Caesalpinioideae) in Africa. *Kirkia* 15: 1-5.
- PEARSON R.S. & BROWN H.P. 1932.—*Commercial timbers of India. Their distribution, supplies, anatomical structure, physical and mechanical properties and uses*. Central Publ. Branch, Govt. of India, 2 vols, Calcutta.
- PRIOR J.A.B. & CUTLER D.F. 1996.—Radial increments in four tropical, drought tolerant firewood species. *Commonwealth Forestry Review* 75: 227-233.
- RAMESH RAO K. & PURKAYASTHA S.K. 1972.—*Indian Woods: Their identification, properties and uses*. Vol. III. Forest Research Institute, Dehra Dun.
- ROSS J.H. 1977.—Caesalpinioideae: 16-19, *Flora of Southern Africa* 16. Botanical Research Institute, Pretoria.
- ROXBURGH W. 1811.—*Plants of the Coast of Coromandel* 3. BULMER W. & Co., London.
- ROY M.M. 1996.—*Hardwickia binata* for silvopastoral systems in India. *Agroforestry Today* 8: 12-13.
- SMITH P.P. & SHAH-SMITH D.A. (in press).—An investigation into the correlation between physical damage and fungal infection/termite activity in *Colophospermum mopane*. *African Journal of Ecology*.
- TAUBERT P. 1894.—Leguminosae: 128-133, in ENGLER & PRANTL, *Nat. Pflanzenf.* III.3. Wilhelm Engelmann, Leipzig.
- TIMBERLAKE J.R. 1995.—*Colophospermum mopane*: Annotated Bibliography and Review. *The Zimbabwe Bulletin of Forestry Research* 11. Forestry Commission, Harare, Zimbabwe.
- VAN ZINDEREN BAKKER E.K. & COETZEE J.A. 1959.—*South African Pollen Grains and Spores*, Part 3: 164-200. Balkema, Amsterdam/Cape Town.
- WHEELER E.A., PEARSON R.G., LA PASHA C.A., ZACK T. & HATLEY W. 1986.—Computer-aided wood identification. Reference manual. *Bull. N. Carolina Agric. Res. Serv.* 474.

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